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12

Exploitative Strategies

Consequences for Individual Behavior, Social Structure, and Design of Institutions

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Abstract

"Exploitation" or free riding are names for strategies by which agents benefit from other agents' investments. This chapter reviews the consequences of these exploitative strategies for individual behavior, social structure, and design of institutions. From an evolutionary perspective, it begins by outlining how natural selection should act to construct behavioral connections that maximize the benefits and minimize the costs of sociality for individuals. Individuals are predicted to show specific leaving or joining decision rules that will construct groups composed of complementary strategies; alternatively, they should be plastic in response to their social environment, which can lead to conditional strategies and social niche construction. What happens on an individual level impacts, in turn, social structures. When individuals have fewer or more frequent interactions with a set of specific (known) individuals, "groupiness" may result to reduce uncertainty in interactions. In humans, common knowledge of within-group norms can further facilitate coordination on socially efficient equilibriums and establish cooperation. Once groups are maintained and cooperate to produce and share resources, they become open to exploitation by other groups, which is directly relevant to the design of institutions. Economic conflict theory offers a potential framework for understanding and predicting exploitative behavior between groups. Through a better understanding of exploitation at these different levels, it is hoped that the payoffs of specific interactions can be adjusted to reduce the negative impacts on a system.

Group photos (top left to bottom right) Michael Kosfeld, Andrew King, Claus Wedekind, Sasha Dall, Kiryl Khalmetski, Bruce Winterhalder, Ben Greiner, Tatsuya Kameda, Andrew King, Wolfgang Leininger, Michael Kosfeld, Ben Greiner, Kiryl Khalmetski, Bruce Winterhalder, Sasha Dall, Claus Wedekind, Tatsuya Kameda, Wolfgang Leininger, Michael Kosfeld and Tatsuya Kameda, Andrew King, Michael Kosfeld

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Introduction

"Social parasitism" (e.g., Cote and Poulin 1995; Safi and Kerth 2007), cheating (e.g., Velicer et al. 2000; Sandoz et al. 2007), or free riding (e.g., Hardin 1968) are all names for strategies by which agents benefit from other agents' investments. Our group was tasked with understanding the consequences of these exploitative strategies for individual behavior, social structure, and design of institutions.

The first obstacle that we faced involved identifying and quantifying exploitation. This is not trivial. Where individuals consistently invest differently in, or receive unequal rewards from, social interaction, counterstrategies tend to evolve which offset or mediate costs (Welbergen and Davies 2009; Kilner and Langmore 2011; Daugherty and Malik 2012). Thus, when we look at the outcome of social interactions across time and contexts, it can be difficult to quantify exploitation because individual behaviors and/or the social system have managed or mitigated it. In other words, there are often scenarios in which it is better for an agent to interact with those that exploit their efforts, or take more than their share, than not to interact with them and get none of the benefits of social interaction. Gaining some benefit is better than getting no benefit at all (West et al. 2006b, 2007c).

To overcome this barrier, we took a Hamiltonian[1] approach (see Figure 12.1) and quantified four types of social interaction (Foster et al. 2001). First, it is useful to distinguish the individual who initiates an interaction from the individual or individuals that it influences (of course there are always consequences for the initiator as well). The former is typically called the *actor* and the latter the *recipient(s)*. Next, assuming that any consequences of actions can be either positive or negative, Hamilton derived a classification scheme that enabled social interactions to be classified into four categories:

1. Mutualism, if the consequences are positive for both actors and recipients
2. Selfishness, if the consequences are positive for the actor but negative for the recipient
3. Altruism, if the consequences are negative for the actor but positive for the recipient
4. Spite, if the consequences are negative for both parties (i.e., actors pay a cost to inflict a cost on recipients)

The strict (original) classification scheme for these four types of social interaction envisages the consequences to lifetime fitness. Many evolutionary ecologists, however, prefer to think instantaneously about the consequences (i.e., accounted to some short-term proxy of fitness like net rate of energy gain)

[1] William Hamilton (1936–2000) was an English evolutionary biologist, widely recognized as one of the most significant evolutionary theorists of the twentieth century.

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		Effect on recipients	
		+	–
Effect on actors	+	Mutualism	Selfishness
	– or 0	Altruism	Spite

Figure 12.1 Classification of social actions, the consequences of which can be either positive or negative.

for such interactions (Barta, this volume). Both views are relevant and applicable here. When juxtaposing the actions of different individuals toward each other in an interaction, mutualistic cooperation (mutual mutualism) can be distinguished from altruistic cooperation (mutual altruism). In a situation where mutual altruism is feasible (West et al. 2007b), we define the term "exploitation" as benefitting from the altruism of another individual without taking an altruistic action. From the perspective of altruistic cooperation, such an action is selfish, since it increases an individual's own payoff (or fitness) at the cost of another's payoff (or fitness). Note that this definition encompasses the producer–scrounger framework (Barnard and Sibly 1981; Vickery et al. 1991), reviewed by Barta (this volume), as well as social dilemma games (e.g., prisoner's dilemma or public goods games) that are studied in economics, reviewed by Burton-Chellew et al. (this volume). When there is no concurrent altruistic action taken by an individual (i.e., when *mutual* cooperation is not feasible), then a selfish action by an individual is not called "exploitative." Exploitation is defined as benefitting from the altruistic cooperation of others.

Now that we have defined selfish social actions that correspond to exploitation as broadly conceived, we can classify, compare, and contrast the consequences of these exploitative strategies for different levels of social organization. Each of these levels will be discussed in turn; for an overview, see Figure 12.2.

Consequences of Exploitation for Individual Behavior

Dubois et al. (this volume) present a broad overview of the behavioral consequences of exploitation and provide an excellent framework for investigating how hoarding (Andersson and Krebs 1978), aggression (Manson and Wrangham 1991; Clutton-Brock and Parker 1995), and coalition formation (Silk 1982) can be caused by the consequences of exploitation. Here, we focus on how the relative frequency of different types of social interactions that individuals experience (Figure 12.2) can play a critical role in their survival and reproduction. Specifically, how frequently and in which contexts an individual interacts with others, with either positive or negative outcomes, can influence the emergence and spread of cooperative behaviors (Gulati 1998; Ohtsuki et al. 2006), social learning (Franz and Nunn 2009; Hoppitt and Laland 2011), and directly transmitted diseases (Newman 2002; Keeling and Eames 2005; Mossong et al. 2008). Consequently, selection should act to construct

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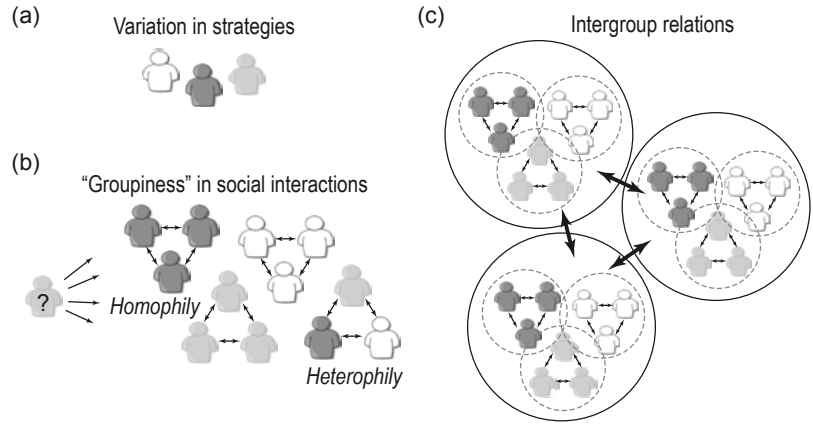

Figure 12.2 Consequences of exploitation for individual behavior, social structure, and the design of institutions. (a) Individuals exhibit between-individual differences in strategy. These strategies need not be fixed. For example, the "white" strategy could be to switch adaptively in accordance with the frequency of behaviors exhibited by the others. (b) Given that interacting individuals vary in their strategies, evolution should select for leaving or joining decision rules that either change group mean (and variance) in strategy or select for individual plasticity in strategy. Both mechanisms function to change strategies to match (homophily) or complement (heterophily) the group. This acts to reduce uncertainty in strategy space, which in turn affects group-level outcomes (e.g., the total amount of food a group acquires). (c) As a result, between-group differences in production and investment emerge, which can lead to intergroup conflicts. Note: populations can also be monomorphic for a strategy but still show individual differences in expressed tactics.

behavioral connections that maximize the benefits and minimize the costs of sociality. In practice this will mean associating with certain individuals and avoiding others; functionally, this will act to reduce uncertainty in their social interactions (Aureli and Vanschaik 1991; Sueur et al. 2011; Farine et al. 2015). Consider a schooling fish, which might interact with thousands of other fish over the course of a day, but tends to form disproportionately close associations with others that are similar to itself in size or activity (Hoare et al. 2000a, b). This may confer increased protection from predators or improve social coordination during migratory movements (Croft et al. 2009). Similarly, while a female baboon will live with many of the same troop mates from birth to death, she will tend to associate with baboons of similar competitive ability (King et al. 2009). This acts to reduce the potential for conflict and increase opportunity for cooperative interaction (King et al. 2008, 2011; King and Sueur 2011), and affects group-level phenotypic composition (Farine et al. 2015).

Group phenotypic composition—or more precisely, the heterogeneity of strategies in groups—can have important implications for individual success

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and fitness (Laskowski and Pruitt 2014; Farine et al. 2015). When individual strategies are fixed—individuals play pure producer or scrounger strategies (Giraldeau and Beauchamp 1999)—selection should result in the evolution of behaviors that will affect heterogeneity of groups—leaving or joining decision rules, or forceful eviction of particular members from groups (Stephens et al. 2005; Kerth et al. 2006; Kerth 2010). In contrast, if strategies are conditional (e.g., Fischbacher et al. 2001) or plastic (Furtbauer et al. 2015) and can be modulated in response to the others—individuals can express varying levels of producing and scrounging in different contexts (Morand-Ferron and Giraldeau 2010)—we expect that selection acts to produce plasticity in response to the social environment. This could lead to social niche construction, whereby individuals alter their associations and interactions with others to increase their chances of surviving and reproducing (Flack et al. 2006; Laskowski and Pruitt 2014; Farine et al. 2015).

Consequences of Exploitation for Social Structure: "Groupiness" and the Reduction of Uncertainty

Dubois et al. (this volume) review the consequences of exploitation for the spatial structure of groups, with a particular focus on the producer–scrounger game. Here, we focus on the consequences of exploitation for social structure (which may or may not be independent of spatial structures) and continue with the theme of flexibility (or plasticity) in strategies using a recent study of producer–scrounger dynamics undertaken by one of our group (Kameda). In this study, people were tasked with finding "treasure" hidden in a 5 × 5 grid, and groups of individuals ($N = 4$) independently decided whether or not to "dig" in one of the grid areas for a treasure, paying some search cost. Each search decision is independent and without communication, so that foragers cannot coordinate their search effort. Importantly, each group member bears the cost of search individually, but a treasure found will be shared evenly by all members. This setup can potentially yield a producer–scrounger situation (see Barta, this volume), where the group production function (i.e., the probability of the treasure to be found) increases monotonically with more cooperators (searchers) but diminishes in margin, because searchers cannot coordinate with each other about where to search (at best, they can only pick up one spot randomly). With feedback about net payoffs and the number of searchers after each round, a phenotypic polymorphism of producers and scroungers emerges. In the first ~33 rounds (except the first round), the producer frequency distributes in a unimodal, almost symmetric distribution. From round ~67 to the end of the experiment (round 100), the distribution of producing across individuals becomes U shaped: roughly 30–40% committed scroungers never cooperate, 20% committed producers almost always cooperate, and the remaining 30% are in-between. Kameda's team then reassigned the subjects to new groups

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as follows: the most cooperative players in each group were assigned to an "elite" group (the most cooperative team), the next most cooperative players into a second group, the third most cooperative players into a third group, and the least cooperative players into the fourth "delinquent" group. Then they played the game again. Although the average cooperation level (proportion of producing) was higher in the "elite" group than in the "delinquent" group, all newly formed groups showed a typical U-shaped distribution. This suggests that the division of producer–scrounger roles in a group is not guided solely by stable social preferences, but is (to some degree) plastic in response to the social environment and can emerge through repeated social interactions. The emergence of U-shaped distributions over time has also been observed in other types of collective tasks by human subjects (Kameda and Nakanishi 2002; Kameda et al. 2011; Toyokawa et al. 2014) and is a necessary outcome where alternative tactics within a population depend on both their frequency and the phenotypes of individuals (Repka and Gross 1995; Gross 1996; Barta and Giraldeau 1998).

Reducing uncertainty in interactions can therefore be achieved by having fewer but more frequent interactions with a set of specific (known) individuals. Where individuals join and leave groups frequently and the system displays high fission–fusion dynamics (Sueur et al. 2011), uncertainty reduction can be achieved via a signal or cue indicative of a particular individual strategy (identity). For instance, in Gouldian finches, *Erythrura gouldiae*, which show two major head-color morphs (red and black), black-headed birds are bolder but less aggressive than red-headed birds (Williams et al. 2012). It has been hypothesized that these head color personality correlations may minimize competitive interactions and facilitate cooperative interactions in groups (Williams et al. 2012; King et al. 2015). Similarly, in species ranging from ants to fish to mammals, group identity can be mediated by olfactory cues (Zenuto and Fanjul 2002; Matsumura et al. 2007) and shared information transmission, including horizontal gene transfer (Ochman et al. 2000), and might be key to explaining the emergence of group identity and resulting cooperative behavior. This is because associations (and thus likelihood of interactions) formed on the basis of such "group identities" or "strategy identities" can reduce the strategic uncertainty that any individual has to face. Work by Ehrhardt and Keser (1999) illustrates how this process may work. In their experiment with human subjects, individuals can endogenously select in which group they interact to play a public goods game (i.e., a multiperson prisoner's dilemma game). They found that cooperators try to be with cooperators, but selfish persons (i.e., exploiters) are constantly chasing the cooperators, which leads to low stability in the groups and a high degree of uncertainty. In Ehrhardt and Keser's setting, cooperators cannot prevent selfish people from joining their group (Charness et al. 2014). Thus, controlling group membership or getting individuals to comply with group-specific behavioral prescriptions (e.g., social norms) can be a means of preserving cooperation within the group.

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In the case of humans, who exhibit strategic behavior (i.e., take into account the strategic rationality of other players), the information structure which mediates the emergence of social norm compliance and mutual cooperation might take more complex forms. In particular, one of the main mechanisms enabling coordination on efficient outcomes in social dilemmas has been shown to be conditional cooperation (Fischbacher et al. 2001), which allows for an evolutionary explanation (Mengel 2008). In this case, a stable cooperation can be achieved only if a given individual *expects* that others will also cooperate. With respect to group identity, this requires coordination not only at the level of first-order beliefs (i.e., beliefs about whether oneself and other individuals belong to a group), but also at the level of second-order beliefs (whether others also *believe* that they belong to the group, and hence might comply with the group norms as well). Otherwise the cooperation of opposing individuals cannot be predicted in advance.

In game theoretic terms, mutual cooperation of conditional players (at least in humans) might therefore require *common knowledge* of group identity. A series of recent laboratory experiments confirmed that common knowledge might be a crucial prerequisite for the emergence of cooperation and prosocial behavior in human groups (thus, truly "activating" group identity), even with minimal group identity (Yamagishi and Mifune 2008; Guala et al. 2013; Ockenfels and Werner 2014). Complementing theoretical work, Gintis (2010) suggests that common knowledge of within-group norms might be interpreted as a purely signaling device, facilitating coordination on socially efficient equilibria and hence self-sufficient for establishing cooperation. Further research in this direction is needed to shed light on the extent to which common knowledge (or similar information structures) might explain the emergence and evolution of real-life cooperation (Henrich et al. 2010).

Another important factor of stability of cooperation within social groups is the perceived *fairness* of internal group rules and procedures; for instance, with respect to the distribution of commonly produced outcome, individual autonomy, or sanctions for defectors (Hartner et al. 2008; Kosfeld et al. 2009; Gaechter and Thöni 2010). Various models suggest several key criteria for assessing fairness in strategic interactions (Fehr and Schmidt 1999; Bolton and Ockenfels 2000; Falk and Fischbacher 2006). At the same time, empirical evidence shows that both individuals and communities strongly vary in their perception of fairness (Henrich et al. 2010; Gelfand et al. 2011). This means that constructing a universal theory of fairness, taking into account its dependence on the situational and institutional context (Henrich et al. 2010; Falk and Szech 2013), still remains an open area for research. In terms of institutional design, a related question is how to reconcile and strengthen the perception of fairness within heterogeneous groups, which might again call for coordinating information structures such as common knowledge of group identity or shared contextual framing (Ellingsen et al. 2012).

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In addition to institutional design, there are both physical (Oliver 1993; King and Sueur 2011) and cognitive (Dunbar 2003; Dunbar and Shultz 2007) limits to maintaining identity in groups, and the benefits of pooling efforts also diminishes in larger group sizes (King and Cowlishaw 2007). Laboratory experiments support this because norm enforcement (e.g., through altruistic punishment of defectors) can be particularly strong in small groups (Henrich et al. 2010; Perc et al. 2013), where a deviation from the group norm is relatively more salient and, hence, more detrimental for the overall group identity. Finally, large groups might be sensitive to the emergence of opportunistic subgroups (characterized by cooperation within the subgroup) but, at the same time, exploit the total group outcome (for further discussion, see Foster et al., this volume). These seemingly contradictory behaviors (prosocial with respect to the subgroup but opportunistic with respect to the whole group) suggest further that intra-(sub)group cooperation might be largely viewed as a pragmatic method of coordination on an efficient outcome, rather than a revelation of altruistic preferences (Guala et al. 2013).

Consequences of Exploitation for Institutions: Intergroup Relations and Economic Conflict Theory

Once groups are maintained and cooperate to produce and share resources, they may become open to exploitation by other groups. Foster et al. (this volume) explore the challenges for market and institutional design when countering exploitation strategies. Here, we take a look at economic conflict theory (ECT) (Hirshleifer 1989, 1991; Skaperdas 1996), which we believe holds much promise for exploring exploitative behavior between groups. The idea behind ECT is to treat appropriative and/or defensive actions as economic activities in their own right. ECT assumes the absence of well-defined property rights in resources and goods in a state of anarchy, which makes expropriation of other owners of resources or goods (through force or otherwise) a viable alternative to own production. Hence there is a trade-off in resource use between productive and appropriative measures. This view goes beyond the scenario of producer–scrounger or hawk–dove games developed in evolutionary biology (see Dubois et al. and Burton-Chellew et al., this volume). These games allow for a dichotomous (extreme) set of actions, but ECT is very applicable to evolutionary analysis with minimal conceptual tweaking.

ECT assumes that two economic agents (which can be individuals, groups, or populations) can combine their resources, R_1 and R_2, in a productive effort to create an additional surplus (consumption good). Evolutionary biologists would refer to this as a public/communal good, and hawk–dove analysis assumes such a communally available resource exists *a priori*. The two agents then have to agree on a division of this surplus. Although their preferences are aligned with regard to the production of the additional surplus (both prefer

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cooperation), they are diametrically opposed with respect to its distribution (each prefers more over less). In the standard economic model with well-established property rights (which, moreover, can be enforced at no cost), rational individuals would peacefully agree on a division through some bargaining procedure, or through a contract that is specified in advance, which is assumed to be enforceable. However, in a state of anarchy without established property rights, the same rational agents would dispute the produced good once it is produced. This provides the rationale to invest part of the resources into "weapons," which increase the likelihood of success in any ensuing conflict over the produced goods. The marginal return on an additional unit of resource invested into weapons is measured by the additional expected winnings from the contest over the produced good. This is smaller now, since one less unit of resources is used in its production, but the probability of winning this smaller "pie" has increased for the investing player. The marginal cost of this additional investment is given by the individual after-fight share of the amount of the good that could have been produced; the latter depends on the productivity of the investing agent. Obviously, the first option—no one invests in weapons and all resources go toward the production of the good—is not an equilibrium.

A conflict technology (contest success function) transforms the investments in weapons made by both players into winning probabilities for both players (Hirshleifer 1989). If neither player invests, a fair division is assumed; investment by only one player leads to a winning probability of "1" for this player. When both players increase their investments into weapons, the amount of resources invested in the production of the good decreases. Symmetric players (i.e., those with identical amounts of the resource and identical productivity) will invest the same amount of resources into weapons. Hence both players win the contest over the produced good with probability 1/2. If $R_1 > R_2$, this result still applies. Hirshleifer (1989, 1991) coined this the *paradox of power*: a poorer agent turns out to be equally powerful in the contest over the produced good. This paradox becomes more pronounced if the agents also differ in productivity for the good: the *more* productive player invests always *less* into weapons in equilibrium than the less productive one. Hence, the *less* productive agent will be *more* powerful in the contest for the produced good and will achieve a higher payoff in equilibrium. Whereas the more productive agent enjoys a comparative advantage in production, the less productive one has the advantage in fighting. This means that productiveness is *inversely* related to power, which is opposite to the case of secure property rights. Moreover, more effective weapons lead to more investments into weapons, and hence lower production and material welfare. Generalizations of this model are provided by Skaperdas (1996) and Hwang (2009).

A slightly more elaborate model allows for the peaceful settlement of the contest over the produced product (Garfinkel and Skaperdas 2006). Suppose that after both agents have invested into weapons and production they bargain over the division of the output. If an agreement is reached at this stage,

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both agents share the good accordingly and the game ends. If no agreement is reached, both agents fight it out with their weapons in a third stage. It is possible to reach agreement at the second stage in the shadow of the conflict that looms ahead (at the third stage). Thus investment into weapons now serves the purpose of gaining an advantageous bargaining position. Clearly, in the bargaining solution, each player must at least receive the amount he can expect from the conflict. The exact division depends on the used bargaining procedure, which also influences investments into weapons.

This model has been adapted to production and conflict between groups (see, e.g., Skaperdas 1998; Wärneryd 1998). Although it is not immediately obvious to us where ECT may apply biologically to a particular species or context, we expect that the same sort of conflict could manifest in life history trade-offs where (say) growing weaponry (or musculature) will diminish the resources available for effort into activities that can produce something that is potentially shareable (Isbell 1991; Berglund et al. 1996). On a longer term, the inverse relationship between productiveness and power, as set out by ECT, gives disincentives to productive innovations and hence stalls growth.

Conclusion

We have managed to go through this chapter with only limited reference to game theoretical models. Mengel and van der Weele, Burton-Chellew et al., and Barta (this volume) provide full details and examples of how these models can be used to understand exploitative strategies. This does not mean that we dismiss this approach; rather the opposite. Research in exploitation by both economists and biologists is related directly or indirectly to the use of game theoretical models. We believe that regular movement back and forth between these models, experimental data, and statistical fitting are necessary to begin to understand how and why exploitation occurs in different biological systems. Systematically classifying any biological system through the use of models may allow us to reverse engineer the key ingredients. Then we may be in a position to manipulate the payoffs and reduce exploitation where this impacts negatively on a system.

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